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THE SELECTION OF TAXONOMIC CHARACTERS FOR MORPHOMETRIC ANALYSIS: A CASE STUDY BASED ON SOUTHERN AFRICAN *AETHOMYS* (MAMMALIA: RODENTIA: MURIDAE)

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ABSTRACT

Prior to a systematic revision of southern African rock rats of the genus *Aethomys* Thomas, statistical procedures were used to select morphometric characters for recording and subsequent use in a revision of the group. The procedure advocated could have wider application in morphometric studies. An initial set of 66 cranial characters was reduced to 51 after the data set was subjected to routine assumptions tests. The remaining 51 characters, considered to be statistically problem-free, were reduced to a final set of 11 characters after subjecting them to cluster and ordination procedures to summarize patterns of correlations between characters, develop criteria for the selection of representative measurements within cluster analysis-generated subclusters, and the subsequent removal of redundant variables. The procedure attempts to economize while at the same time adequately represent the phenotype, an approach consistent with the concept of morphological integration. Four additional cranial and four standard external characters are also included in the final data set, but for descriptive and comparative purposes only.

INTRODUCTION

African rock rats of the genus *Aethomys* are endemic to east, west, central, and southern Africa where the genus is represented by ten species (Wilson and Reeder, 1993). Five species, *A. namaquensis, A. silindensis, A. granti, A. nyikae,* and *A. chrysophilus* are currently recognized in southern Africa (Meester et al., 1986; Skinner and Smithers, 1990), but the latter species has been shown to include two forms based on chromosome (Gordon and Rautenbach, 1980; Gordon and Watson, 1986; Visser and Robinson, 1986; Baker et al., 1988), electrophoresis (Gordon and Watson, 1986), and sperm morphology (Gordon and Watson, 1986; Visser and Robinson, 1987; Breed et al., 1988). Schlitter (1978) considered the genus in critical need of revision.

The present paper forms part of a revision of southern African species of *Aethomys,* and in particular examines the selection of quantitative taxonomic characters, a critical but often neglected step in many systematic studies (Strauss and Bookstein, 1982; Rohlf, 1990). In small mammals, no established procedure is available for selecting appropriate character sets. Approaches used to date generally fall into four categories: 1) selection of character sets that have been used in the past, often with the ad hoc addition or deletion of characters after elementary correlation analysis (Power, 1971; Chapman et al., 1992); 2) selection of as many measurements as practicable (Watson and Dippenaar, 1987; Chimimba

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and Kitchener, 1991), reflecting the influence of numerical taxonomy as advocated in Sneath and Sokal (1973); 3) selection based on an assessment of functional units of the cranium (Taylor, 1990; Taylor and Meester, 1993); and 4) selection of landmarks as advocated in the most recent developments in morphometrics (Strauss and Bookstein, 1982; Bookstein et al., 1985; Zelditch et al., 1989; Rohlf and Bookstein, 1990; Rohlf and Marcus, 1993).

Although characters selected on the basis of the first two categories can perform well, it is important to assess character redundancy in morphometric studies (Blackith and Reyment, 1971; Sneath and Sokal, 1973; Thorpe, 1976; James and McCulloch, 1990; Rohlf, 1990). Nevertheless, apart from a few studies (Thomas, 1968; Best, 1978; Taylor, 1990; Taylor and Meester, 1993), it has been rarely considered in practice. The utilization of unevaluated characters could have a profound effect on analyses (Pimentel and Smith, 1986*b*), ranging from distortion of inter-Operational Taxonomic Unit (OTU: Sneath and Sokal, 1973) relationships (Blackith and Reyment, 1971) to an increase in analysis time that often results in analytical problems while processing large data matrices (Chimimba and Kitchener, 1991). Some studies have shown that after the assessment of linear dependence (redundancy) and colinearity, sets of many quantitative characters can be reduced to a few and still contain equivalent information (Mahalanobis et al., 1949; Albrecht and Blackith, 1957).

Various approaches that have been used to screen for reliable characters include either analysis of variance (ANOVA) or correlations between characters (Pimentel and Smith, 1986*b*). The former procedure is restricted to multigroup studies in which character redundancy is sometimes ignored (Pimentel and Smith, 1986*b*). The latter approach summarizes correlations between characters by principal component (PCA), factor (Thomas, 1968; Johnston, 1973; Gould et al., 1974) and cluster analyses (Power, 1971; Taylor, 1990; Taylor and Meester, 1993) with the selection of characters from within highly correlated subsets of characters. Another strategy has been to employ Mahalanobis' (1936) D^2 statistic (Thorpe, 1976), a similarity coefficient that takes into account the degree of information redundancy in each character as summarized by the within-group covariance. However, owing to the instability of correlation coefficients for sample sizes smaller than 20, Van Valen (1974) considered this an oversimplification (Thorpe, 1976).

The approach used in the present study stems from current theory of evolutionary change that emphasizes the unity of the genotype (Mayr, 1963, 1976; Lewontin, 1974; Wright, 1978, 1980) in which organisms are the integrated functional units that evolve (Waddington, 1957; Riedl, 1978; Gould and Lewontin, 1979; Selzer, 1993; Borgia, 1994). Embryological studies have, for instance, demonstrated that the cranium represents a functional character suite that interacts and has a common ontogenetic origin (Noden, 1978, 1983; Gans and Northcutt, 1983; Zelditch et al., 1993). Olson and Miller (1958) hypothesized, and subsequently demonstrated, that the degree of cranial integration can be measured by the intensity of statistical associations in the phenotype. Therefore, developmentally and functionally related traits ought to be relatively highly correlated in the phenotype. On both empirical and theoretical grounds these authors placed developmentally and functionally interdependent morphological characters into "Functional sets" ("F-sets"). Empirically derived sets of characters that were relatively highly correlated were placed into "Phenotypic sets" ("P-sets"). Other studies support the a priori-defined morphologically integrated functional units

of Olson and Miller (1958) (Moss and Young, 1960; Cheverud, 1982; Cheverud et al., 1989; Cane, 1993). Taylor (1990) and Taylor and Meester (1993) extended the morphological integration concept into a character selection protocol.

The present study is aimed at selecting meaningful morphometric characters for use in a revision of southern African *Aethomys*. Accordingly, the procedure of Taylor (1990) and Taylor and Meester (1993), which summarized character correlations in the yellow mongoose (*Cynictis penicillata*, Viverridae) by cluster analysis, is expanded upon to meet three important requirements: 1) "comprehensiveness" (i.e., the consideration of adequate coverage of the phenotype), 2) "economy" (by the removal of redundant characters), and 3) "pattern summary" (of relationships between characters consistent with the morphological integration concept of Olson and Miller, 1958). Southern African *Aethomys* is here used as a case study for this character selection protocol that could find wider application in morphometric studies of other taxa.

Recent developments in landmark-based methods (Mousseau, 1991; Rohlf and Marcus, 1993), especially their extension to three-dimensional space, suggest a modification of the morphological integration concept, involving a more rigorous morphometric assessment of functional units (Van der Klaauw, 1948–1952) based on landmarks (rather than measuring points) and a closer integration with more recent advances in ontogenetic cranial development (Thorogood and Tickle, 1988).

MATERIAL AND METHODS

The present study is based mainly on a single homogeneous sample, representing an island population of *Aethomys namaquensis* (21 males, 13 females) from Keimoes Island, Orange River, Cape Province, but additional samples of *A. granti* (seven males, seven females) from Sutherland, Cape Province, and *A. chrysophilus* (six males, ten females) from Maasstroom, Transvaal, were used to develop criteria for the selection of the final set of measurements. The material examined is listed in Appendix I.

Individuals were assigned to seven toothwear classes (with reference to Morris, 1972; Perrin, 1982; Dippenaar and Rautenbach, 1986), but to reduce the effect of age variation, only adult, toothwear class VI (Chimimba and Dippenaar, 1994) individuals with complete data sets were considered.

An initial set of 66 linear cranial (40 skull, nine mandible, and 17 dental) measurements (Fig. 1a–k) were recorded by one observer (CTC) to the nearest 0.05 mm using a pair of Fowler digital calipers, a Fowler Interface and EASYCAL program developed by S. Reig for direct data input to rBase (Ashton-Tate Software, Inc., USA). While the character set reflects an attempt to distribute measurements across functional units of the skull, this was not always possible because of constraints imposed by the use of calipers and the taxonomic need to include traditional characters which were not selected on the basis of the morphological integration concept. Owing to the unreliability of external characters, only cranial characters were considered.

Univariate and multivariate data screening (Pimentel and Smith, 1986*a*, 1986*b*; Reig, 1989) revealed two male specimens with outlier values not consistent with toothwear class VI. One was exceptionally large (USNM 451966) in most measurements and the other (USNM 452055) had an abnormally small greatest cross-sectional crown width of M_3 (66-WMT). To avoid the introduction of bias in the

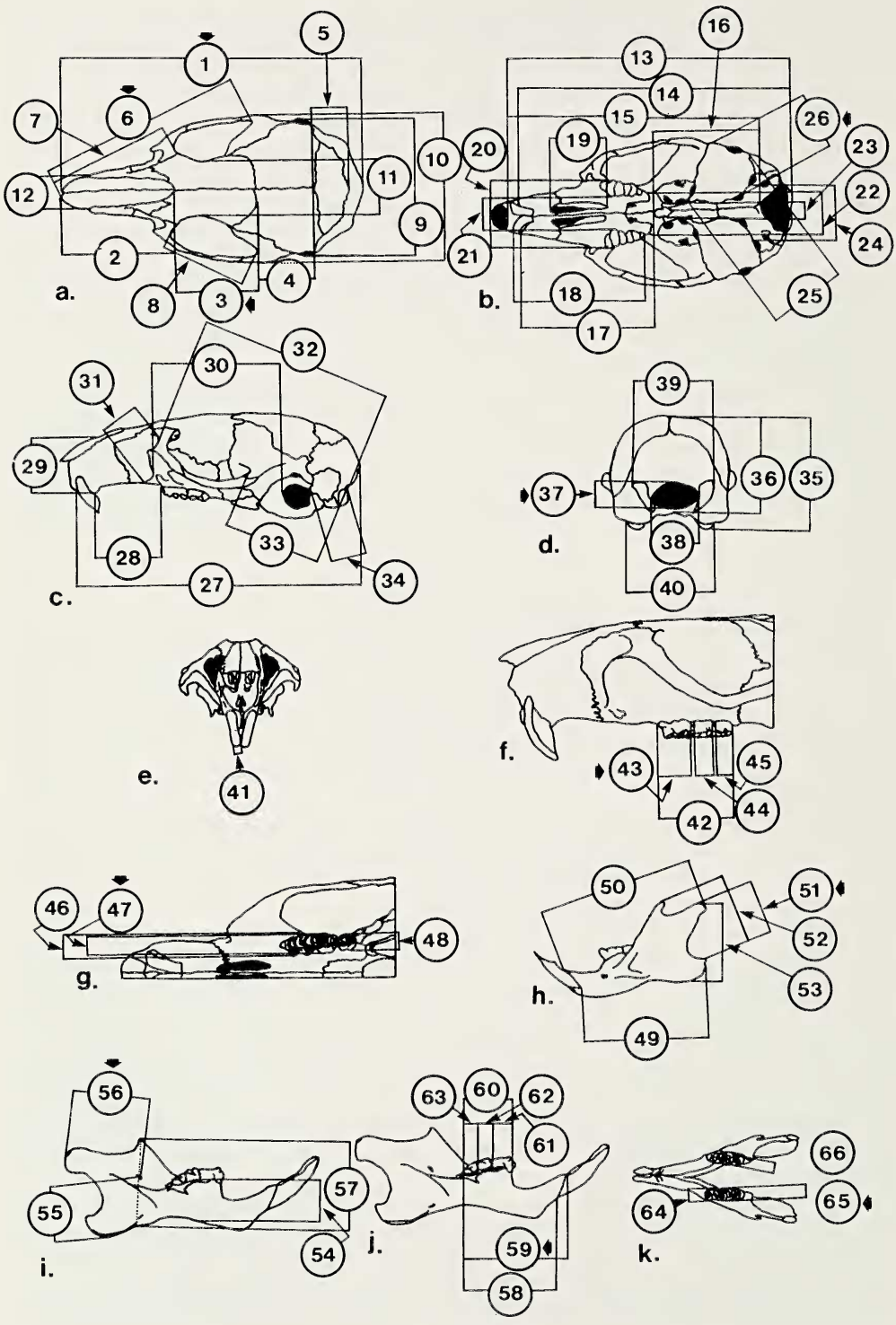
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Fig. 1.—Reference points of cranial measurements. Asterisks indicate measurements used in original descriptions.

a. *1-GLS—Greatest length of skull, from anterior edge of nasals to posterior edge of occipital condyle, along longitudinal axis of skull; 2-GLN—Greatest length of nasals, from longest posterior projection of nasal wings to anteriormost edge of nasal bones; *3-FRO—Greatest length of frontals; *4-PAR—Greatest length of parietals; *5-INT—Interparietal length, from intersection of sagittal suture and posterior end of parietal, perpendicular to posterior end of interparietal; 6-NPP—Distance from anterior edge of nasals to anterior edge of posterior part of zygomatic arch; 7-NPO—Distance from anterior edge of nasals to posterior edge of postorbital bar; 8-ZAL—Zygomatic arch length, from posteriormost part of anterior part of zygomatic arch to anteriormost part of posterior part of zygomatic arch; *9-BBC—Breadth of braincase—width at dorsal root of squamosals; *10-ZYW—Greatest zygomatic width, between outer margins of zygomatic arches, perpendicular to longitudinal axis of skull; *11-IOB—Least breadth of interorbital constriction—least distance dorsally between orbits; *12-NAS—Nasal width, at anteriormost point where nasals join premaxillae.

b. 13-CBL—Condylobasal length of skull, from posteriormost projection of occipital condyles to anterior edge of premaxillae; *14-PIC—Incisor to condyle length, from posterior surface of I^1 at alveolus to posteriormost projection of occipital condyle; *15-BSL—Basal length of skull, from anteriormost point of lower border of foramen magnum to anterior edge of premaxilla; *16-PPL—Postpalatal length, from anteriormost edge of hard palate to anteriormost point on lower border of foramen magnum; *17-PAL—Palatilar length, from posterior edge of I^1 alveolus to posterior edge of hard palate; 18-TRL—Toothrow length, from anterior alveolus to posterior surface of M^3 alveolus; *19-LPF—Greatest length of longest palatal foramen; *20-MAW—Greatest maxillary width between labial crown edges of M^1; *21-PWM—Hard palate width at M^1 measured on lingual side of teeth at alveolus; 22-PAC—Hard palate width at point of constriction immediately posterior to M^3; 23-VCW—Vidian canal width at foramen lateral to pterygoid processes; 24-FJW—Least distance between foramina jugulare on posterior edge of bullae; *25-BUL—Greatest bulla length at 45° angle to skull axis; *26-BUW—Greatest bulla width at 45° angle to skull axis.

c. *27-ITC—Incisor to condyle length, from anterior surface of I^1 at alveolus to posteriormost projection of the occipital condyle; *28-LOD—Length of diastema, from posterior base of I^1 alveolus to anterior base of M^1 alveolus; 29-HOR—Height of rostrum, perpendicularly from a point directly behind incisors; 30-IOE—Distance from anterior base of zygomatic plate to anterior edge of ear opening; 31-IZD—Infraorbital–zygomatic plate distance, from dorsal edge of infraorbital foramen to anterior base of zygomatic plate; 32-MPO—Foramen magnum–postorbital bar length, from lateral edge of foramen magnum (at notch in lateral view) to anterior edge of postorbital bar; 33-MPZ—Foramen magnum–zygomatic arch length, from lateral edge of foramen magnum (at notch in lateral view) to anterior edge of posterior part of zygomatic arch; 34-FME—Foramen magnum–external auditory meatus length, from lateral edge of foramen magnum (at notch in lateral view) to posterodorsal edge of external auditory meatus.

d. *35-GHS—Greatest height of skull perpendicular to horizontal plane through bullae; 36-BCH—Braincase height, from dorsal surface of sagittal crest to midventral surface of basioccipital between anterior bullae; 37-FMH—Foramen magnum height—widest part of foramen in vertical plane; 38-FMW—Foramen magnum width—widest part of foramen magnum in a horizontal plane; 39-CNW—Greatest occipital condyle width perpendicular to skull axis; 40-WAB—Width at bullae on ear openings perpendicular to skull axis.

e. 41-FIB—I^1 breadth—breadth of principal upper incisor at level of median edge of alveolus.

f. 42-UTR—Crown length of maxillary toothrow, from anterior edge of M^1 at alveolus to posterior edge of M^3 at alveolus; 43-LFM—Length of M^1 along cingulum; 44-LSM—Length of M^2 along cingulum; 45-LTM—Length of M^3 along cingulum.

g. 46-WFM—Greatest cross-sectional crown width of M^1; 47-WSM—Greatest cross-sectional crown width of M^2; 48-WTM—Greatest cross-sectional crown width of M^3.

h. *49-GML—Greatest mandible length, in a straight line, from anterior edge of I_1 alveolus to posterior surface of angular process; *50-MDL—Greatest length of mandible (excluding teeth), from posterior surface of condylar process to anteroventral edge of incisor alveolus; 51-AFA—Angular process–mandibular condyle length, in straight line from ventral edge of angular process to middorsal ridge of mandibular condyle; 52-MRH—Mandible–ramus height, from dorsal edge of coronoid process to ventral edge of angular process; 53-MCA—Mandibular condyle–angular process distance, in straight line from dorsal edge of mandibular condyle to ventral edge of angular process.

i. 54-LMH—Least mandible height, perpendicularly from between posterior M_1 alveolus and anterior M_2 alveolus; 55-MFA—Mandibular foramen–angular process length, from anterior edge of

sample, the two specimens were considered as not representative of the population, and excluded from subsequent analyses.

Homoscedasticity was tested for by Hartley's (1950) F_{max}-test (Sokal and Rohlf, 1981) and a one-way analysis of variance (ANOVA) was used to assess sexual dimorphism. Skewness (g_1), kurtosis (g_2), and normality (Chi-square test) also were tested for (Zar, 1974; Sokal and Rohlf, 1981; Pimentel and Smith, 1986*a*, 1986*b*).

Following Cheverud (1982), character associations were investigated by cluster analysis of principal component (PCA) scores generated from standardized, statistically problem-free characters. Results of three Q-mode principal components analyses (sexes pooled and separate) of correlations among all OTUs were similar so that only the pooled sample is considered below. The first 14 components (explaining 99.98% of the sample variance) were retained and Euclidean distances between each pair of characters subjected to Ward's (1963) hierarchical clustering algorithm to generate phenotypic sets (P-sets). This algorithm produces homogeneous clusters by minimizing the squared positional variation of elements in a cluster independently at each step (Cheverud, 1982).

Selection of characters from within the cluster analysis-generated subclusters depended on six ancillary criteria in the following order of priority: (1) relative weightings of characters in R-mode principal component (Thorpe, 1980; Gould, 1984; James and McCulloch, 1990) and correspondence analyses (Benzecri, 1977; Greenacre, 1984, 1986, 1990) of three known species, *A. chrysophilus, A. granti,* and *A. namaquensis*; (2) consideration of coefficients of variation (CV) incorporating Haldane's (1955) correction (Sokal and Rohlf, 1981); (3) measurement error (ME) (Ostle and Mensing, 1975; Pankakoski et al., 1987; Bailey and Byrnes, 1990; Lougheed et al., 1991) expressed as percentage of total variability due to *within*-individual variation (percent measurement error [% ME]), based on three independent sets of repeated measurements recorded by CTC on separate occasions for *A. namaquensis*; (4) relative ease of measurement; (5) measuring points associated with frequently damaged areas of the skull (with reference to analyses that require complete data sets; Kim, 1975; Klecka, 1975); (6) previous use, particularly in original descriptions.

All analyses were undertaken with BIOΣTAT I and II (Pimentel and Smith, 1986*a*, 1986*b*), UNIVAR (Power, 1970), STATGRAPHICS (STSC Inc., USA) and SimCA (Greenacre, 1990).

Morphological cranial terminology follows Thomas (1905), Hill (1935), Hall (1946), Rosevear (1969), Hebel and Stromberg (1976), DeBlase and Martin (1981), and DeGraaff (1981).

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mandibular foramen to posterior edge of angular process; 56-MAF—Mandibular foramen–articular facet length, from ventral edge of mandibular foramen to midposterodorsal edge of articulating facet; *57-CMH—Coronoid mandible height, from dorsal edge of coronoid process to ventral edge of mandible in line with mandibular foramen.

j. 58-MTL—Mandibular toothrow, from anterior edge of I_1 alveolus to posterior edge of M_3 alveolus; 59-IML—Posterior incisor–M_3 length, in a straight line from posterior edge of I_1 alveolus to posterior edge of M_3 alveolus; 60-MTR—Mandibular toothrow length, from anterior edge of M_1 alveolus to posterior edge of M_3 alveolus; 61-LLM—Length of M_1, along cingulum; 62-LMS—Length of M_2, along cingulum; 63-LMT—Length of M_3, along cingulum.

k. 64-WLM—Greatest cross-sectional crown width of M_1; 65-WMS—Greatest cross-sectional crown width of M_2; 66-WMT—Greatest cross-sectional crown width of M_3.

RESULTS

Univariate Screening of Measurements

Hartley's (1950) F_{max}-test for homogeneity of variances between males and females of *A. namaquensis* indicated significant ($P < 0.05$) heteroscedasticity in four measurements, 19-LPF, 20-MAW, 38-FMW, and 50-MDL (see Figs. 1a–k for measurements; univariate statistics are available on request either from the first author or the Transvaal Museum Library).

Descriptive statistics and results of a one-way analysis of variance indicated a generally low level of sexual dimorphism in *A. namaquensis,* with significant differences in only six of the 66 characters: 4-PAR ($P < 0.05$), 21-PWM ($P < 0.05$), 31-IZD ($P < 0.01$), 51-AFA ($P < 0.01$), 53-MCA ($P < 0.01$), and 57-CMH ($P < 0.01$). This finding justified the pooling of sexes in subsequent analyses.

Results of tests for skewness and kurtosis based on the pooled male and female sample of *A. namaquensis* showed three of the 66 characters to be both skewed and kurtotic: 34-FME (both $P < 0.01$), 38-FMW ($P < 0.05$ and $P < 0.001$, respectively), and 50-MDL (both $P < 0.05$). One character, 65-WMS, was skewed only ($P < 0.05$). Three characters were kurtotic only: 49-GML ($P < 0.01$), 55-MFA ($P < 0.05$), and 62-LMS ($P < 0.001$).

Chi-square tests for normality in the pooled male and female sample of *A. namaquensis* showed that 26 of the 66 characters were non-normally distributed: 2-GLN ($P < 0.01$), 4-PAR ($P < 0.05$), 7-NPO ($P < 0.05$), 9-BBC ($P < 0.05$), 11-IOB ($P < 0.05$), 12-NAS ($P < 0.01$), 16-PPL ($P < 0.05$), 17-PAL ($P < 0.01$), 23-VCW ($P < 0.001$), 26-BUW ($P < 0.05$), 28-LOD ($P < 0.01$), 29-HOR ($P < 0.001$), 31-IZD ($P < 0.05$), 34-FME ($P < 0.05$), 38-FMW ($P < 0.001$), 40-WAB ($P < 0.05$), 41-FIB ($P < 0.001$), 47-WSM ($P < 0.05$), 49-GML ($P < 0.001$), 51-AFA ($P < 0.05$), 55-MFA ($P < 0.05$), 56-MAF ($P < 0.05$), 57-CMH ($P < 0.05$), 61-LLM ($P < 0.01$), 62-LMS ($P < 0.001$), 66-WMT ($P < 0.01$). These results may reflect the instability of this class of tests when sample sizes are small, but draw attention to potentially problematic characters.

After the assumptions tests, the following highly conservative criteria were used to either reject or retain a character: (1) a character was rejected if it differed significantly at the 5% level in more than one test; (2) a character was rejected if it was significant in one or more tests at the 1% level of significance; and (3) a character was retained if test statistics for sexual dimorphism, homoscedasticity, and normality did not differ significantly, or were significant in one of the three tests but only at the 5% level of significance. As a consequence, 15 potentially problematic characters were rejected (2-GLN, *12-NAS, *17-PAL, 23-VCW, *28-LOD, 29-HOR, 34-FME, 38-FMW, 41-FIB, *49-GML, *50-MDL, 55-MFA, 61-LLM, 62-LMS, 66-WMT, which included the five traditional characters indicated by asterisks). Although sample sizes were small for this class of tests, reconsideration of the 15 characters indicated that most were problematic with respect to one or more of the following: (1) unclearly defined recording points, which made the placement of caliper tips difficult and therefore subject to error; (2) high variability between individuals; and (3) association with frequently damaged parts of the skull.

Analysis of Character Associations

In the phenogram derived from Ward's (1963) cluster analysis of the 51 remaining characters, three relatively discrete character groupings are apparent (Fig.

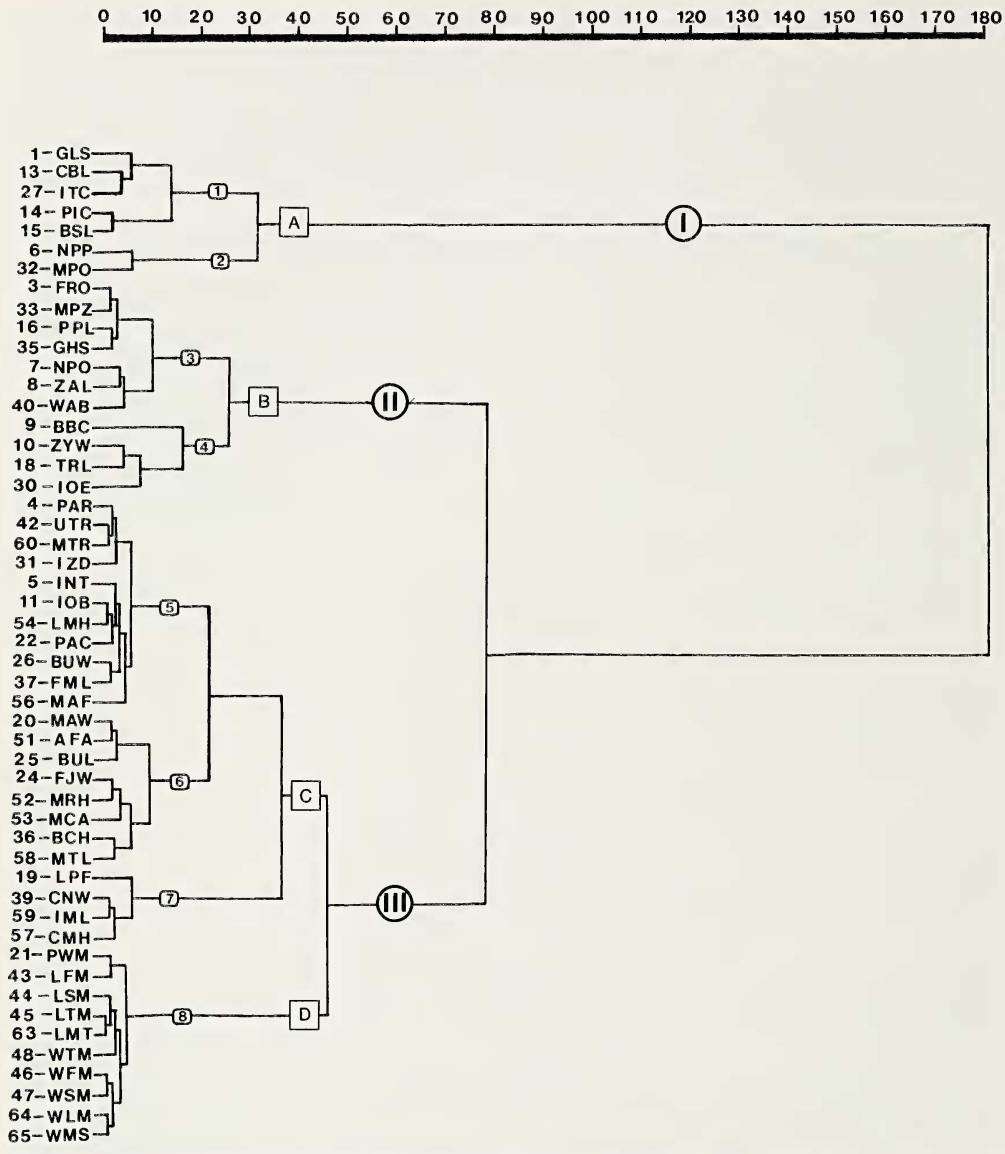

Fig. 2.—Phenogram depicting relationships between cranial measurements in *Aethomys namaquensis*. Clusters formed at the three-, four- and eight-cluster stages are indicated by enclosed letters and numbers. Characters are defined in Fig. 1a–k. The cophenetic correlation coefficient is 0.81.

2). The three major clusters, designated I, II, and III, are summarized in Table 1. Although some characters are apparently not related to the majority of characters within a given subset (indicated by question marks in Table 1), subclusters at both the four- and eight-cluster stages in general form logical subsets. Major cluster I relates mainly to what may be termed a "Mixed" Neurocranial/orofacial functional set (F-set). Characters in this major cluster reflect size-related measurements that span the major functional units of the skull, if not the entire length of the skull. This cluster of characters is further subdivided into a subcluster

comprising "Longitudinal distances" (1) and the other comprising "Oblique distances" (2).

Major cluster II relates mainly to the Neurocranial functional set. Although there are no clear demarcations at the eight-cluster stage in terms of three partially independent submatrices (frontal, parietal, and occipital; Cheverud, 1982) of the Neurocranial functional set, characters in subcluster 3 include measurements of the dorsal side of the cranium and various measurements related to the configuration of the braincase itself, the exception being 8-ZAL which belongs to the orbital submatrix of the Orofacial functional set. Subcluster 4 also includes two measurements related to the configuration of the braincase, as well as upper toothrow length (18-TRL), which belongs to the dental phenotypic set in the Orofacial functional set, and distance from anterior base of zygomatic plate to anterior edge of ear opening (30-IOE) of "Mixed" Orofacial/neurocranial origin.

Major cluster III relates mainly to the Orofacial functional set. Most characters (23 of 33) collectively fit into orbital/oral/masticatory phenotypic set in the Orofacial functional set. In cluster C, subcluster 5 includes measurements of the lateral region of the rostrum, the orbital and postpalatal regions and the toothrows, and one mandibular measurement, while almost all mandibular measurements appear in subclusters 6 and 7. Of interest is that almost all measurements related to the bullae and the foramen magnum also appear in cluster C.

Most prominent at the eight-cluster stage is subcluster 8, which, with the exception of hard palate width at M^1 (21-PWM), are masticatory characters joining up at relatively low distances, suggestive of a tightly integrated dental submatrix.

Selection of Measurements

One of the criteria developed to select measurements from within subclusters relied on ordinations, both principal component (Fig. 3) and correspondence (Fig. 4) analyses, of known taxa (*A. namaquensis, A. chrysophilus,* and *A. granti*). The first two axes from the principal component analysis show *A. granti* to separate from both *A. chrysophilus* and *A. namaquensis* along the second axis, whereas the latter two species are separated from each other along the first axis; there was little or no differentiation between the three taxa along components 3 to 14. Principal component I generally has high and negative loadings on all measurements (Table 1), with generally high percent variances associated with each character's component contribution (in parentheses in Table 1). This suggests that the separation between *A. chrysophilus* and *A. namaquensis* is primarily size-related. The second axis, which is instrumental in separating *A. granti* from both *A. chrysophilus* and *A. namaquensis,* has character loadings and percent variances of different magnitudes (the former with different signs), suggesting shape-related variation. The important characters with relatively high loadings (regardless of sign) on the second axis are: 3-FRO, 4-PAR, 5-INT, 6-NPP, 26-BUW, 31-IZD, 37-FMH, 47-WSM, 53-MCA, 56-MAF, 58-MTL, 59-IML, and 65-WMS.

Two-dimensional symmetric profiles from correspondence analysis (Fig. 4), with individuals from the same taxon enclosed in minimum convex polygons, show clear separation among the three species along both principal axes I (Inertia = 25.27% and $\lambda_1 = 0.0004$) and II (20.59%; $\lambda_2 = 0.0003$). A plot of individual characters, which allows examination of the level of association between rows (in this case, individuals) and columns (characters), is superimposed on the same figure. The scattergram shows that separation of the three taxa can be explained in terms of the corresponding opposition of the following characters in the planes

Table 1.—*Principal component (PCA) (including percent variance contributions, in parentheses) and principal coordinate (CA) (in permills) loadings for the first two axes, coefficients of variation (CV), and percent measurement error (% ME) for each character. Letters and numbers to the left indicate clusters formed at the three-, four- and eight-cluster stages of the cluster analysis. Characters followed by a question mark do not belong in the particular functional (F-set) or phenotypic (P-set) set. Characters in parentheses were important in principal components and correspondence analyses. Underlined characters were selected for descriptive and comparative purposes. Characters preceded by an asterisk were selected for use in subsequent morphometric analyses. Characters are defined in Fig. 1a–k.*

Character/F-set	PCA I	PCA II	CA I	CA II	CV	% ME
I. "MIXED" NEUROCRANIAL/OROFACIAL F-SET						
A. (Interfrontal, -parietal, and -occipital)						
1. "Incisor–condyle distances"						
*1-GLS	−0.957 (91.65)	0.130 (1.69)	11	−3	1.93	0.013
13-CBL	−0.959 (91.93)	0.130 (1.68)	10	−1	2.02	0.014
27-ITC	−0.973 (94.71)	0.049 (0.24)	4	−3	1.05	0.015
14-PIC	−0.974 (94.84)	−0.074 (0.55)	−2	−8	2.02	0.008
15-BSL	−0.968 (93.63)	−0.026 (0.07)	−3	1	2.53	0.014
2. "Oblique distances"						
*(6-NPP)	−0.856 (73.23)	0.294 (8.66)	26	−13	2.18	0.014
32-MPO	−0.857 (97.50)	0.026 (0.07)	−1	5	1.91	0.014
II. NEUROCRANIAL F-SET						
B. (Braincase and dorsal part of skull)						
3. *(3-FRO)	−0.668 (44.60)	0.594 (35.23)	63	50	4.44	0.006
33-MPZ	−0.973 (94.60)	−0.050 (0.25)	−18	22	2.49	0.013
16-PPL	−0.947 (89.61)	0.061 (0.37)	−3	22	3.08	0.012
35-GHS	−0.892 (79.59)	0.239 (5.71)	14	1	2.71	0.010
7-NPO	−0.888 (78.89)	0.154 (2.38)	16	−4	3.32	0.015
8-ZAL ?	−0.941 (88.47)	0.085 (0.73)	9	−9	2.14	0.012
40-WAB	−0.941 (88.64)	0.033 (0.11)	2	1	2.55	0.014
4. 9-BBC	−0.952 (90.60)	−0.010 (0.01)	−3	−1	2.91	0.008
10-ZYW	−0.977 (95.43)	−0.070 (0.49)	−12	8	2.34	0.015
18-TRL ?	−0.971 (94.25)	−0.134 (1.81)	−9	−6	2.11	0.014
30-IOE ?	−0.959 (91.91)	0.177 (3.13)	7	22	1.82	0.014
III. OROFACIAL F-SET						
C. (Oral and orbital cavities, exoccipital bullae)						
5. (4-PAR ?)	−0.797 (63.53)	−0.301 (9.06)	−40	−1	7.34	0.008
42-UTR	−0.905 (81.89)	−0.040 (0.16)	−15	3	3.71	0.013
60-MTR	−0.827 (68.39)	0.061 (0.37)	3	−10	2.43	0.006
(31-IZD)	−0.615 (37.85)	0.500 (24.97)	49	19	6.65	0.014
(5-INT ?)	−0.345 (11.92)	−0.714 (51.00)	−62	−64	9.55	0.007
11-IOB	−0.898 (80.70)	−0.142 (2.02)	−12	0	2.81	0.013
54-LMH	−0.904 (81.74)	0.106 (1.12)	−2	19	5.44	0.009
22-PAC	−0.720 (51.90)	0.105 (1.11)	10	−15	5.55	0.015
*(26-BUW ?)	−0.865 (74.76)	−0.250 (6.25)	−35	8	3.73	0.001
*(37-FMH ?)	−0.436 (19.03)	0.437 (19.07)	36	−30	4.90	0.012
*(56-MAF)	−0.421 (17.73)	−0.662 (43.77)	−48	−55	5.60	0.013
6. 20-MAW	−0.943 (88.21)	−0.047 (0.22)	−1	−12	2.98	0.013
*(51-AFA)	−0.934 (87.22)	−0.147 (2.17)	−63	75	5.52	0.010
25-BUL ?	−0.855 (73.17)	0.003 (0.01)	−7	9	4.64	0.012
24-FJW ?	−0.718 (51.58)	−0.050 (0.25)	4	−23	5.45	0.008
52-MRH	−0.781 (60.93)	0.113 (1.28)	5	14	5.87	0.011
(53-MCA)	−0.850 (72.32)	−0.254 (6.43)	−21	−5	4.36	0.006
36-BCH ?	−0.900 (80.91)	0.035 (0.12)	3	−8	2.93	0.013
(58-MTL)	−0.866 (75.06)	−0.374 (14.00)	−35	−7	3.89	0.008
7. 19-LPF ?	−0.722 (52.10)	0.152 (2.31)	18	−13	5.00	0.013

Table 1.—*Continued.*

Character/F-set	PCA I	PCA II	CA I	CA II	CV	% ME
39-CNW ?	−0.886 (78.43)	−0.190 (3.60)	36	−14	3.82	0.013
*(59-IML)	−0.905 (81.93)	−0.314 (9.86)	−21	−12	3.01	0.011
57-CMH	−0.887 (78.74)	−0.133 (1.78)	−12	−1	3.56	0.006
D. (Dental)						
8. 21-PWM ?	−0.787 (61.91)	−0.099 (0.98)	−16	24	7.98	0.013
*(43-LFM)	−0.896 (75.48)	−0.126 (1.58)	−37	19	6.12	0.013
(44-LSM)	−0.736 (54.13)	−0.048 (0.23)	−62	94	12.99	0.005
(45-LTM)	−0.665 (44.27)	−0.202 (4.08)	−22	−15	7.10	0.007
63-LMT	−0.644 (41.45)	−0.129 (1.67)	−12	−3	6.98	0.005
48-WTM	−0.670 (44.87)	−0.044 (0.19)	−7	−9	6.52	0.013
(46-WFM)	−0.478 (22.90)	0.184 (3.38)	18	−42	5.19	0.014
*(47-WSM)	−0.475 (22.59)	0.339 (11.48)	24	−31	5.78	0.011
64-WLM	−0.704 (49.51)	0.208 (4.34)	12	−22	5.39	0.010
*(65-WMS)	−0.501 (25.11)	0.580 (33.68)	39	−16	4.62	0.012

% Trace: 68.4% (PC Axis I); 6.4% (PC Axis II).
Inertia: 25.3% ($\lambda_1 = 0.0004$) (CA Axis I); 20.6% ($\lambda_2 = 0.0003$) (CA Axis II).

of separation: 3-FRO, 4-PAR, 5-INT, 6-NPP, 26-BUW, 31-IZD, 37-FMH, 43-LFM, 44-LSM, 45-LTM, 46-WFM, 47-WSM, 51-AFA, 53-MCA, 56-MAF, 58-MTL, 59-IML, and 65-WMS. Characters important in the separation of the three taxa are shown by their relatively high magnitudes in the first and second principal coordinates (Table 1), which for ease of interpretation are presented in permills (thousandths).

The results of the principal component and correspondence analyses correspond closely in that the 13 shape-related characters generated by the second principal component were also generated by the two principal coordinates in correspondence analysis, in which the following characters also featured prominently: 43-LFM, 44-LSM, 45-LTM, 46-WFM, and 51-AFA.

Table 1, in which characters are arranged according to cluster analysis-derived phenotypic sets, summarizes the data used in character selection, including coefficients of variation, percent measurement error values, character loadings on the first and second axes of principal component, and correspondence analyses. Other criteria invoked were relative ease of measurement, potential for non-missing values, previous use, and cranial configuration. Based on the premise that most subclusters represent distinct submatrices of either the Neurocranial or the Orofacial functional unit, one or more characters were selected as representative of the configuration of a particular unit. More than one character was often selected, particularly if the characters were consistently shown to be relevant by both the principal component and correspondence analyses, and these included obviously misplaced characters.

The following is the rationale behind the selection of characters within a subcluster (with subcluster numbering corresponding to the eight-cluster stage in Fig. 2 and Table 1):

Subcluster 1.—The notion that shape is more heritable than size (Humphries et al., 1981) has been criticized by Leamy and Thorpe (1984). Size is certainly important in infraspecific studies. For example, in a principal component analysis of different populations of *C. penicillata,* Taylor (1990) and Taylor and Meester (1993) found that virtually all the significant variation was in the first size-related

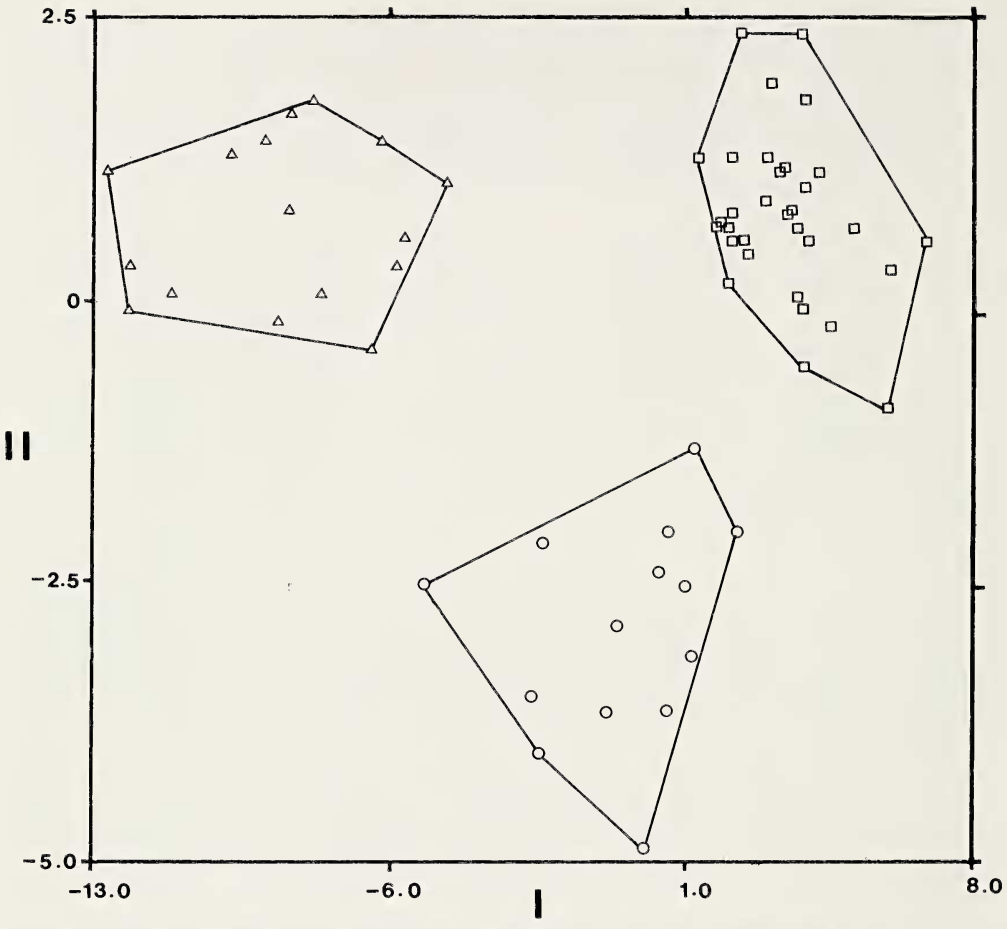

Fig. 3.—First two components from principal components analysis of individuals of *Aethomys chrysophilus,* open triangle; *A. granti,* open circle; and *A. namaquensis,* open square. Polygons include individuals from the same taxon.

axis. Consequently one character from subcluster 1, comprising size-related characters, was selected for inclusion in the basic data suite. High loadings on the first principal component axis (>0.90) indicate that all characters in this major cluster qualify as good predictors of general size. In addition, all the characters have low coefficients of variation and percent measurement error values. However, the greatest length of the skull (1-GLS) was selected because of its relatively high loading on the first principal coordinate in correspondence analysis, relative ease of measurement, and the fact that it features prominently in rodent systematics. This character, in combination with cranial width and depth measurements (see below), also captures descriptive information relating to gross cranial configuration.

Subcluster 2.—Distance from anterior edge of nasals to anterior edge of posterior part of zygomatic arch (6-NPP) was selected because it featured prominently in the first principal coordinate in correspondence analysis. It has relatively low coefficient of variation and percent measurement error values and being an "oblique" measurement, may capture different configurations of the skull.

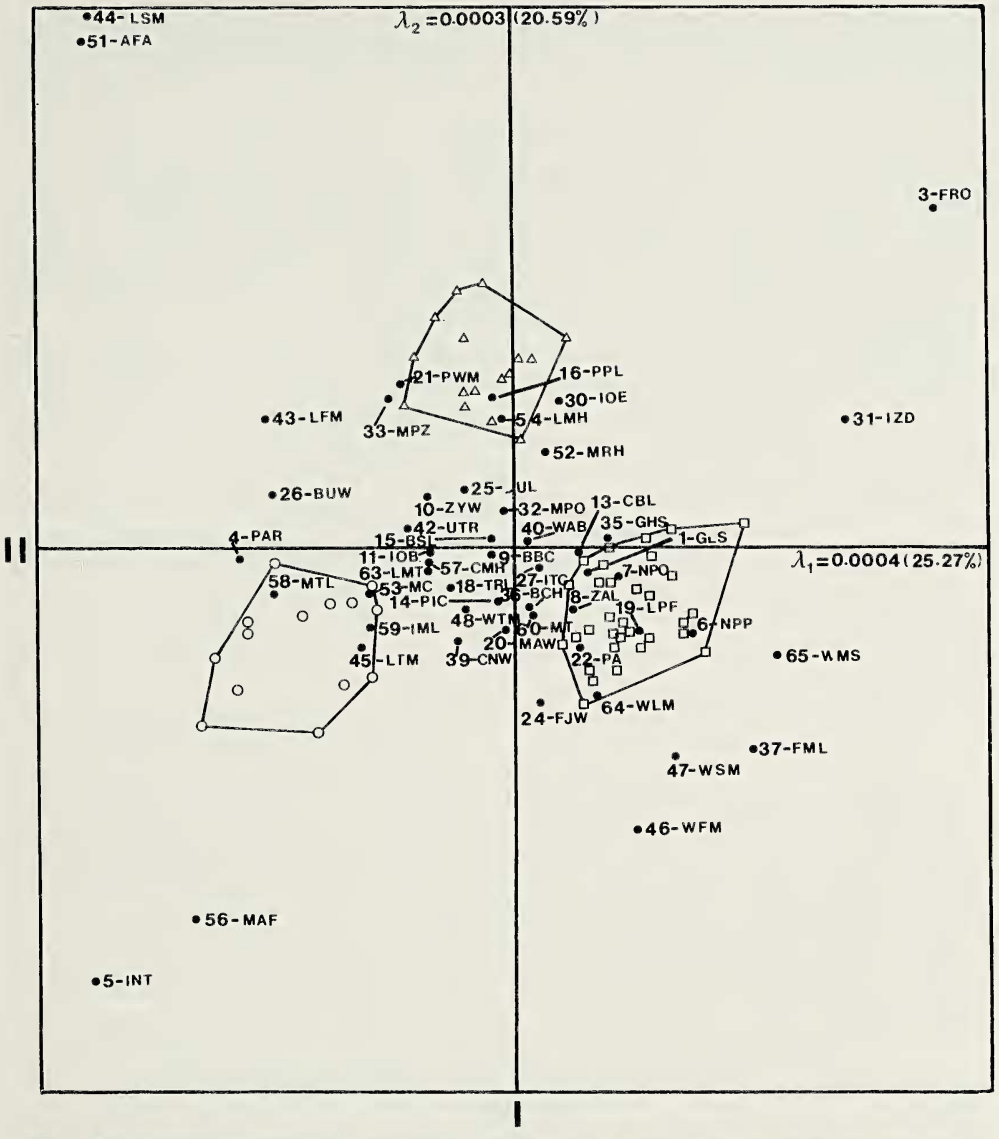

Fig. 4.—Optimal two-dimensional symmetrical map of characters and individuals generated by correspondence analysis of *Aethomys chrysophilus,* open triangle; *A. granti,* open circle; and *A. namaquensis,* open square. Polygons include individuals from the same taxon. Characters are defined in Fig. 1a–k.

Subcluster 3.—Of the seven characters in this subcluster, greatest length of frontals (3-FRO) is the only character selected. In addition to having low coefficient of variation and percent measurement error values, it was consistently singled out by both axes in correspondence analysis as well as the second component of principal component analysis. It also features prominently in original descriptions.

Subcluster 4.—None of the four characters in this subcluster was shown to be of particular relevance, but see discussion on the selection of descriptive characters below.

Subcluster 5.—The following three characters in this subcluster were selected: greatest bulla width (26-BUW), foramen magnum height (37-FMH), and mandibular foramen–articular facet length (56-MAF), all of which were shown to be of importance, either singly or in combination, by both principal coordinates in correspondence analysis and principal component II in principal component analysis. These characters also have low coefficients of variation and percent measurement error values. Collectively, the three characters capture different configurations of the skull, as suggested by the negative and positive loadings, respectively, of foramen magnum height (37-FMH) and mandibular foramen–articular facet length (56-MAF) on the second principal component. Greatest bulla width (26-BUW) features prominently in original descriptions.

Subcluster 6.—Angular process–mandibular condyle length (51-AFA), one of the eight characters in this subcluster, was selected because of its importance in principal coordinate I in correspondence analysis, and low coefficient of variation and percent measurement error values. Mandibular toothrow (58-MTL) is another character shown to be of importance, but see discussion of subcluster 7.

Subcluster 7.—Of the four characters in this subcluster, posterior incisor–M_3 length (59-IML) was selected because of its low coefficient of variation and percent measurement error values and its importance in both correspondence (coordinate I) and principal component (component II) analyses. This character, as well as mandibular toothrow (58-MTL) in subcluster 6, although placed in different subsets, seem to capture the same information, but since the latter measurement is relatively difficult to score, 59-IML was selected.

Subcluster 8.—Three characters in this subcluster were selected: length of M^1 (43-LFM), and greatest cross-sectional crown widths of M^2 (47-WSM) and M_2 (65-WMS) because of their low coefficients of variation and percent measurement error values and their importance (either singly or in combination) in principal coordinates I and II of correspondence analysis, and principal component II of principal component analysis. In combination (an upper jaw tooth length [43-LFM] and width [47-WSM] and lower jaw tooth width [65-WMS]) they may improve the capturing of different tooth configurations.

Three of the 11 selected characters (indicated by asterisks in Table 1 and broad arrows in Fig. 1a–k), 1-GLS, 3-FRO, and 26-BUW, feature prominently in original descriptions.

The underlined characters in Table 1 were selected for descriptive purposes only and include breadth of braincase (9-BBC), greatest height of skull (35-GHS), interorbital constriction (11-IOB), and greatest bulla length (25-BUL). These characters, in combination with greatest length of skull (1-GLS), capture gross cranial configuration. Other descriptive characters incorporated into the data set were the standard external measurements, head and body length, tail length, hind foot length, and ear length, all recorded from specimen labels.

Given the three groupings of characters (11 basic cranial, four descriptive cranial, and four standard descriptive external), their selective use (singly or in combination) will depend on the choice of analyses to be used in the revision. Since multivariate procedures involve the assessment of joint relationships among intercorrelated variables to evaluate overall inter-OTU differences (James and McCulloch, 1990), all subsequent multivariate analyses will be based on the 11 basic cranial characters, and will form the basis of taxonomic conclusions in the revision. The four descriptive cranial characters, in combination with the 11 basic cranial characters, could be used for exploratory multivariate analyses. Univariate analyses, which evaluate the equality of means for each variable independently

and ignore correlations among variables (Willig et al., 1986), could be based on all three groupings of characters, and only used for descriptive and comparative purposes.

DISCUSSION

The approach to character selection adopted in the present paper is an extension of the procedure suggested by Taylor (1990) and Taylor and Meester (1993) who summarized character correlations in *C. penicillata* by means of cluster analysis, and selected representative characters on the basis of low coefficients of variation, previous use, and ease of measurement, and interpreted their results in terms of the morphological integration concept of Olson and Miller (1958). As applied to *Aethomys,* the approach was similar to Taylor (1990) and Taylor and Meester (1993), but expanded upon to include: 1) measuring potentially useful characters from various regions of the cranium and mandible (including characters used previously) in a single homogeneous sample, representing an island population; 2) screening the data set for outliers; 3) subjecting all characters to univariate assumptions tests (normality, equality of variances, and sexual dimorphism); followed by 4) analysis of statistical associations between characters, using principal component and cluster analyses, with reference to a morphometric assessment of functional units of the cranium, an approach consistent with the morphological integration concept of Olson and Miller (1958); and 5) analysis of samples drawn from various taxa in the current classification as an aid in the selection of characters from identified phenotypic sets and their subsets, while considering criteria such as the coefficient of variation, percent measurement error, ease of recording, and previous use.

The procedures followed by Taylor (1990), Taylor and Meester (1993), and the present study are more objective than using untested, previously used characters or simply recording as many characters as possible in the hope of assessing relationships between OTUs. These approaches could have wider application in morphometrics, particularly in organisms in which cranial ontogenetic origins and interactions (Noden, 1978, 1983; Gans and Northcutt, 1983; Zelditch et al., 1993), structural components, evolution, and adaptive functional potential of organismic form can be determined, such as has been demonstrated in some mammalian (Olson and Miller, 1958; Moss and Young, 1960; Moore, 1981; Cheverud, 1982) and avian groups (Noden, 1978, 1983; Cane, 1993).

Analysis of the largest available sample of southern African *Aethomys* from a single locality, representing an island population of *A. namaquensis,* identified two outliers that were considered as not representative of the population and were excluded from the data set to avoid the introduction of bias in the sample. The assumptions tests identified 15 characters as statistically problematic because they were significantly sexually dimorphic, heteroscedastic, and/or non-normally distributed; these results could be related a posteriori to difficulties experienced in their recording, unclearly defined measuring points in some individuals, high variability of characters among individuals, and characters associated with frequently damaged parts of the skull. Interestingly, some of the characters that were found to be problematic have been used extensively in previous studies (Smith, 1834; Roberts, 1951; Ellerman et al., 1953; Meester et al., 1986; Skinner and Smithers, 1990), such as nasal width (12-NAS), palatal length (17-PAL), length of diastema (28-LOD), greatest mandible length (from anterior edge of I_1 alveolus to posterior surface of angular process) (49-GML), and from anteroventral edge of I_1 alveolus to posterior surface of condylar process (50-MDL). The data screen-

ing procedures underscore Pimentel and Smith's (1986*b*) remarks that test statistics are particularly useful in the earliest phases of data analysis in taxonomic studies.

The results of cluster analysis of character associations were encouraging insofar as the major Neurocranial and Orofacial functional units were identified. In this respect, the results are similar to those obtained by Cheverud (1982), Taylor (1990), and Taylor and Meester (1993). Apart from these functional units, some measurements, particularly the length measurements traditionally used by taxonomists (e.g., condylobasal length), did not fit into the above units but formed a major cluster by themselves comprising "Mixed" Neurocranial/orofacial characters. In *C. penicillata,* these "Mixed" measurements were placed in the Neurocranial functional set (Taylor, 1990; Taylor and Meester, 1993) rather than in a separate major cluster as in *Aethomys.*

The primary objective of the study was to evaluate new and previously used characters in order to identify a reduced set of measurements which would summarize most important variations of cranial configuration. Since many of the measurements spanned the major functional units of the cranium, it was not surprising that the classification of measurements was equivocal. However, the analysis did generate highly correlated subsets of measurements, particularly in the case of dental characters. Strong indications of logical subsets were also evident in: 1) the configuration of the braincase and dorsal aspect of the skull; and 2) the orbital/oral/masticatory functional submatrices with which, interestingly, characters related to the bullae and foramen magnum were also associated.

Ancillary to the analysis of character associations, analysis of known taxa was undertaken to develop criteria for the selection of representative characters from within the phenotypic sets generated by cluster-analysis. This step was considered necessary since the analysis of character associations did not produce unequivocal groupings of characters, and because it is also not yet clear how tightly individual functional units are integrated in the phenotype. Final selection of 11 basic measurements to be used for the revision of southern African *Aethomys* was also made with reference to coefficients of variation, measurement error, likelihood of damage, and use by previous authors. The 11 measurements are: greatest length of skull (1-GLS), greatest length of frontals (3-FRO), distance from anterior edge of nasals to anterior edge of posterior part of zygomatic arch (6-NPP), greatest bulla width (26-BUW), foramen magnum height (37-FMH), length of M^1 (43-LFM), greatest cross-sectional crown width of M^1 (47-WSM), angular process–mandibular condyle length (51-AFA), mandibular foramen–articular facet length (56-MAF), posterior incisor–M_3 (59-IML), and greatest cross-sectional crown width of M_2 (65-WMS). With regard to coefficients of variation, all characters had low values for this statistic except greatest length of parietals (4-PAR), interparietal length (5-INT), hard palate width at M^1 (21-PWM), infraorbital–zygomatic plate distance (31-IZD), length of M^2 (44-LSM) and M^3 (45-LTM), greatest cross-sectional crown width of M^3 (48-WTM), and length of M_3 (63-LMT), while percent measurement error showed this parameter to be negligible in all characters recorded. In contrast, percent measurement error values of over 50% have been recorded in recent studies on birds and mussels (Bailey and Byrnes, 1990).

Principal component and correspondence analyses were used to develop criteria for the selection of representative characters, and both showed a broad concordance between characters shown to be of relevance. Canonical variates analysis (Pimentel, 1979; Campbell and Atchley, 1981; Livezey, 1989, 1990; Livezey and

Storer, 1992) was also considered but in an analysis of the 51-character data set a singular dispersion matrix was encountered, and analysis could not proceed (Pimentel and Smith, 1986*b*). Similar computational difficulties were encountered by Taylor (1990) and Taylor and Meester (1993) in a 48-variable matrix. This may be related to: 1) large numbers of linearly and colinearly constrained variables (Pimentel and Smith, 1986*b*); 2) the presence of ipsative variables (Pimentel, 1979); and 3) the sample size being much smaller relative to number of variables (Williams and Titus, 1988). This finding emphasizes the possibility of encountering analytical problems when using many unscreened variables in morphometric studies (Blackith and Reyment, 1971).

With the recent introduction of sophisticated three-dimensional measuring equipment and recent advances in unit-free, landmark-based morphometric methods (Strauss and Bookstein, 1982; Rohlf and Bookstein, 1990, and references therein; Rohlf and Marcus, 1993), future development of character selection protocols should focus on a clearer demarcation of the functional units of the cranium in relation to the individual cranial elements, and on synergism between landmark selection and the objectives of both species delineation and higher classification. In the present study the emphasis was on the former objective, while a different set of qualitative data will be used for phylogenetic analysis. The emphasis should also shift to a rigorous assessment of traditional characters. This is already apparent in the present study where some of these characters were included simply for descriptive purposes and for comparison with previous studies, particularly with reference to their utility in relating morphometric results to the nomenclature.

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LITERATURE CITED

ALBRECHT, F. O., AND R. E. BLACKITH. 1957. Phase and molting polymorphism in locusts. Evolution, 11:166–177.

BAILEY, R. C., AND J. BYRNES. 1990. A new, old method for assessing measurement error in both univariate and multivariate morphometric studies. Systematic Zoology, 39:124–130.

BAKER, R. J., M. B. QUMSIYEH, AND I. L. RAUTENBACH. 1988. Evidence for eight tandem and five centric fusions in the evolution of the karyotype of *Aethomys namaquensis* A. Smith (Rodentia: Muridae). Genetica, 76:161–169.

BENZECRI, J. P. 1977. Histoire et préhistoire de l'analyse des données. 5-L'analyse des correspondances. Cahiers de l'Analyse des Données, 2:9–40.

BEST, T. L. 1978. Variation in Kangaroo rats (Genus *Dipodomys*) of the *heermanni* group in Baja California, Mexico. Journal of Mammalogy, 59:160–175.

BLACKITH, R. E., AND R. A. REYMENT. 1971. Multivariate Morphometrics. Academic Press, London, 412 pp.

BOOKSTEIN, F. L., B. C. CHERNOFF, R. L. ELDER, J. M. HUMPHRIES, G. R. SMITH, AND R. E. STRAUSS. 1985. Morphometrics in Evolutionary Biology. Special Publication No. 15, Academy of Natural Sciences of Philadelphia, Philadelphia, 277 pp.

BORGIA, G. 1994. The scandals of San Marco. Quarterly Review of Biology, 69:373–375.

BREED, W. G., G. A. COX, C. M. LEIGH, AND P. HAWKINS. 1988. Sperm head structure of a murid rodent from southern Africa: The red veld rat *Aethomys chrysophilus*. Gamete Research, 19:191–202.

CAMPBELL, N. A., AND W. R. ATCHLEY. 1981. The geometry of canonical variates analysis. Systematic Zoology, 30:268–280.

CANE, W. P. 1993. The ontogeny of postcranial integration in the common tern, *Sterna hirundo*. Evolution, 47:1138–1151.

CHAPMAN, J. A., K. L. KRAMER, N. J. DIPPENAAR, AND T. J. ROBINSON. 1992. Systematics and biogeography of the New England cottontail, *Sylvilagus transitionalis* (Bangs, 1895), with description of a new species from the Appalachian Mountains. Proceedings of the Biological Society of Washington, 105:841–866.

CHEVERUD, J. M. 1982. Phenotypic, genetic, and environmental morphological integration in the cranium. Evolution, 36:499–516.

CHEVERUD, J. M., G. P. WAGNER, AND M. M. DOW. 1989. Methods for the comparative analysis of variation patterns. Systematic Zoology, 38:201–213.

CHIMIMBA, C. T., AND N. J. DIPPENAAR. 1994. Non-geographic variation in *Aethomys chrysophilus* (De Winton, 1897) and *A. namaquensis* (A. Smith, 1834) (Rodentia: Muridae) from southern Africa. South African Journal of Zoology, 29:107–117.

CHIMIMBA, C. T., AND D. J. KITCHENER. 1991. A systematic revision of Australian Emballonuridae (Mammalia: Chiroptera). Records of the Western Australian Museum, 15:203–265.

DEBLASE, A. F., AND R. E. MARTIN. 1981. A Manual of Mammalogy, with Key to Families of the World. Wm. C. Brown Company Publishers, Dubuque, Iowa, 329 pp.

DEGRAAFF, G. 1981. The Rodents of Southern Africa. Butterworths, Pretoria, 267 pp.

DIPPENAAR, N. J., AND I. L. RAUTENBACH. 1986. Morphometrics and karyology of the southern African species of the genus *Acomys* I. Geoffroy Saint-Hilaire, 1838 (Rodentia: Muridae). Annals of the Transvaal Museum, 34:129–183.

ELLERMAN, J. R., T. C. S. MORRISON-SCOTT, AND R. W. HAYMAN. 1953. Southern African Mammals 1758 to 1951: A Reclassification. British Museum of Natural History, London, 363 pp.

GANS, C., AND R. G. NORTHCUTT. 1983. Neural crest and the origin of vertebrates: A new head. Science, 220:268–273.

GORDON, D. H., AND I. L. RAUTENBACH. 1980. Species complexes in medically important rodents: Chromosome studies of *Aethomys, Tatera* and *Saccostomus* (Rodentia: Muridae, Cricetidae). South African Journal of Science, 76:559–561.

GORDON, D. H., AND C. R. B. WATSON. 1986. Identification of cryptic species of rodents (*Mastomys, Aethomys, Saccostomus*) in the Kruger National Park. South African Journal of Zoology, 21:95–99.

GOULD, S. J. 1984. Covariance sets and ordered geographic variation in *Cerion* from Aruba, Bonaire and Curacao: A way of studying non-adaptation. Systematic Zoology, 33:217–237.

GOULD, S. J., AND R. LEWONTIN. 1979. The spandrels of San Marco and the Panglossian paradigm: A critique of the adaptionist program. Proceedings of the Royal Society of London, B205:581–598.

GOULD, S. J., D. F. WOODRUFF, AND J. P. MARTIN. 1974. Genetics and morphometrics of *Cerion* at Pongo Carpet: A new systematic approach to this enigmatic land snail. Systematic Zoology, 23:518–535.

GREENACRE, M. J. 1984. Theory and Applications of Correspondence Analysis. Academic Press, London, 364 pp.

———. 1986. SimCA: A program to perform simple correspondence analysis. American Statistician, 40:230–231.

———. 1990. SimCA, User's Manual. Department of Statistics, University of South Africa (UNISA), Pretoria, 44 pp.

HALDANE, J. B. S. 1955. The measurement of variation. Evolution 9:484.

HALL, E. R. 1946. Mammals of Nevada. University of California Press, Berkeley and Los Angeles, 710 pp.

HARTLEY, H. O. 1950. The maximum *F*-ratio as a short cut test for heterogeneity of variances. Biometrika, 37:308–312.

HEBEL, R., AND M. W. STROMBERG. 1976. Anatomy of the Laboratory Rat. Williams and Wilkens, Baltimore, 173 pp.

HILL, J. E. 1935. Cranial foramina in rodents. Journal of Mammalogy, 16:121–129.

HUMPHRIES, J. M., F. L. BOOKSTEIN, B. CHERNOFF, G. R. SMITH, R. L. ELDER, AND S. G. POSS. 1981. Multivariate discrimination by shape in relation to size. Systematic Zoology, 30:291–308.

JAMES, F. C., AND C. E. MCCULLOCH. 1990. Multivariate analysis in ecology and systematics: Panacea or Pandora's box? Annual Review of Ecology and Systematics, 21:129–166.

JOHNSTON, R. E. 1973. Evolution in the house sparrow. IV. Replicate studies in phenetic covariation. Systematic Zoology, 22:219–226.

KIM, J. O. 1975. Factor analysis. Pp. 468–514, *in* Statistical Package for the Social Sciences (N. H. Nie, C. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent, eds.), McGraw-Hill Book Company, New York, 675 pp.

KLECKA, W. R. 1975. Discriminant analysis. Pp. 434–467, *in* Statistical Package for the Social Sciences (N. H. Nie, C. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent, eds.), McGraw-Hill Book Company, New York, 675 pp.

LEAMY, L., AND R. S. THORPE. 1984. Morphometric studies in inbred and hybrid house mice. Heterosis, homeostasis and heritability of size and shape. Biological Journal of the Linnean Society, 22:233–241.

LEWONTIN, R. 1974. The Genetic Basis of Evolutionary Change. Columbia University Press, New York, 346 pp.

LIVEZEY, B. C. 1989. Morphometric patterns in recent and fossil penguins (Aves, Sphenisciformes). Journal of Zoology, London, 219:269–307.

———. 1990. Evolutionary morphology of flightlessness in the Auckland Islands teal. Condor, 92: 639–673.

LIVEZEY, B. C., AND R. W. STORER. 1992. Morphometric comparison of skeletons on the western grebe complex *Aechmophorus* of the United States and Canada. Condor, 94:668–679.

LOUGHEED, S. C., T. W. ARNOLD, AND R. C. BAILEY. 1991. Measurement error of external and skeletal variables in birds and its effect on principal components. Auk, 108:432–436.

MAHALANOBIS, P. C. 1936. On the generalized distance in statistics. Proceedings of the National Institute of Science (India), 2:49–55.

MAHALANOBIS, P. C., D. M. MAJUMDAR, AND C. R. RAO. 1949. Anthropometric survey of the United Provinces, 1941; a statistical study. Sankhya, 3:35–40.

MAYR, E. 1963. Animal Species and Evolution. Harvard University Press, Cambridge, Massachusetts, 797 pp.

———. 1976. Evolution and the Diversity of Life. Harvard University Press, Cambridge, Massachusetts, 719 pp.

MEESTER, J. A. J., I. L. RAUTENBACH, N. J. DIPPENAAR, AND C. M. BAKER. 1986. Classification of southern African mammals. Transvaal Museum Monograph, 5:1–359.

MOORE, W. J. 1981. The Mammalian Skull. Cambridge University Press, Cambridge, England, 369 pp.

MORRIS, P. 1972. A review of mammalian age determination methods. Mammal Review, 2:69–104.

MOSS, M. L., AND R. W. YOUNG. 1960. Functional approach to craniology. American Journal of Physical Anthropology, 18:281–292.

MOUSSEAU, T. A. 1991. Landmarks in morphometrics, or the shape and size of morphometrics to come. Evolution, 45:1979–1980.

NODEN, D. 1978. The control of avian cephalic neural crest cytodifferentiation. I. Skeletal and connective tissues. Developmental Biology, 67:296–312.

———. 1983. The embryonic origin of avian cephalic and cervical muscles and associated connective tissues. American Journal of Anatomy, 168:257–276.

OLSON, E. C., AND R. L. MILLER. 1958. Morphological Integration. University of Chicago Press, Chicago, 317 pp.

OSTLE, B., AND R. W. MENSING. 1975. Statistics in Research. Third Edition. Iowa State University Press, Ames, 596 pp.

PANKAKOSKI, E., R. A. VAISANEN, AND K. NURMI. 1987. Variability of muskrat skulls: Measurement error, environmental modification and size allometry. Systematic Zoology, 36:35–51.

PERRIN, M. R. 1982. Prey specificity of the barn owl, *Tyto alba,* in the Great Fish River Valley of the eastern Cape Province. South African Journal of Wildlife Research, 12:14–25.

PIMENTEL, R. A. 1979. Morphometrics: The Multivariate Analysis of Biological Data. Kendall/Hunt Publishing Company, Dubuque, Iowa, 276 pp.

PIMENTEL, R. A., AND J. D. SMITH. 1986*a*. BIOΣTAT I. A Tutorial Manual. Sigma Soft, Placentia, California, 392 pp.
———. 1986*b*. BIOΣTAT II. A Tutorial Manual. Second Edition. Sigma Soft, Placentia, California, 212 pp.
POWER, D. M. 1970. Geographic variation of red-winged blackbirds in central North America. University of Kansas. Publications of the Museum of Natural History, 19:1–83.
———. 1971. Statistical analysis of character correlations in Brewer's blackbirds. Systematic Zoology 20:186–203.
REIG, S. 1989. Errors and misjudgment of outliers in morphometric studies. Abstract of Papers and Posters, Fifth International Theriological Congress, Rome.
RIEDL, R. 1978. Order in Living Organisms. John Wiley and Sons, New York, 313 pp.
ROBERTS, A. 1951. The Mammals of South Africa. Trustees of "The Mammals of South Africa" Book Fund, Johannesburg, 700 pp.
ROHLF, F. J. 1990. Morphometrics. Annual Review of Ecology and Systematics, 21:299–316.
ROHLF, F. J., AND F. L. BOOKSTEIN, EDS. 1990. Proceedings of the Michigan Morphometrics Workshop. Special Publication No. 2, University of Michigan Museum of Zoology, Ann Arbor, 380 pp.
ROHLF, F. J., AND L. F. MARCUS. 1993. A revolution in morphometrics. Trends in Ecology and Evolution, 8:129–132.
ROSEVEAR, D. R. 1969. The Rodents of West Africa. British Museum of Natural History, London, 604 pp.
SCHLITTER, D. A. 1978. Problems and priorities of research on the taxonomy and ecology of African small mammals. Pp. 211–214, *in* Ecology and Taxonomy of African Small Mammals (D. A. Schlitter, ed.), Bulletin of Carnegie Museum of Natural History, 6, 214 pp.
SELZER, J., ED. 1993. Understanding Scientific Prose: Rhetoric of the Human Sciences. University of Wisconsin Press, Madison, 388 pp.
SKINNER, J. D., AND R. H. N. SMITHERS. 1990. The Mammals of the Southern African Subregion. University of Pretoria, Pretoria, 771 pp.
SMITH, A. 1834. African zoology: Mammalia. South African Quarterly Journal, 2:160.
SNEATH, P. H. A., AND R. R. SOKAL. 1973. Numerical Taxonomy. W. H. Freeman, San Francisco, 573 pp.
SOKAL, R. R., AND F. J. ROHLF. 1981. Biometry. Second Edition. W. H. Freeman and Company, New York, 859 pp.
STRAUSS, R. E., AND F. L. BOOKSTEIN. 1982. The truss: Body form reconstructions in morphometrics. Systematic Zoology, 31:113–135.
TAYLOR, P. J. 1990. Infraspecific systematics of the yellow mongoose. Unpublished Ph.D. thesis, University of Natal, Durban, 345 pp.
TAYLOR, P. J., AND J. MEESTER. 1993. Morphometric variation in the yellow mongoose, *Cynictis penicillata* (Cuvier, 1829) (Carnivora: Viverridae) in southern Africa. Durban Museum Novitates, 18:37–71.
THOMAS, O. 1905. Suggestions for the nomenclature of the cranial length measurements and of the cheek-teeth of mammals. Proceedings of the Biological Society of Washington, 18:191–196.
THOMAS, P. A. 1968. Variation and covariation in characters of the rabbit tick, *Haemaphysalis leporipalustris*. Kansas University Science Bulletin, 47:829–862.
THOROGOOD, P., AND C. TICKLE, EDS. 1988. Cranial Development: Papers Presented at a Meeting of the British Society for Developmental Biology, University of Bath, 1987. The Company of Biologists Ltd, Cambridge, 257 pp.
THORPE, R. S. 1976. Biometric analysis of geographic variation and racial affinities. Biological Review, 51:407–457.
———. 1980. A comparative study of ordination techniques in numerical taxonomy in relation to racial variation in the ringed snake *Natrix natrix* (L.). Biological Journal of the Linnean Society, 13:7–40.
VAN DER KLAAUW, C. J. 1948–1952. Size and position of the functional components of the skull. Archives Neerlandaises de Zoologie, 9:1–559.
VAN VALEN, L. 1974. Multivariate structural statistics in natural history. Journal of Theoretical Biology, 45:235–257. *Erratum* (1974), 48:501.
VISSER, D. S., AND T. J. ROBINSON. 1986. Cytosystematics of the South African *Aethomys* (Rodentia: Muridae). South African Journal of Zoology, 21:264–268.
———. 1987. Systematic implications of spermatozoan and bacular morphology for the South African *Aethomys*. Mammalia, 51:447–454.
WADDINGTON, C. 1957. The Strategy of the Genes. Allen and Unwin, London, 262 pp.

WARD, J. 1963. Hierarchical grouping to optimize an objective function. Journal of the American Statistics Association, 58:236–243.

WATSON, J. P., AND N. J. DIPPENAAR. 1987. The species limits of *Galerella sanguinea* (Ruppell, 1836), *G. pulverulenta* (Wagner, 1839) and *G. nigrata* (Thomas, 1928) in southern Africa (Carnivora: Viverridae). Navorsinge van die Nasionale Museum Bloemfontein, 5:356–413.

WILLIAMS, B. K., AND K. TITUS. 1988. Assessment of sampling stability in ecological applications of discriminant analysis. Ecology, 69:1275–1285.

WILLIG, M. R., R. D. OWEN, AND R. L. COLBERT. 1986. Assessment of morphometric variation in natural populations: The inadequacy of the univariate approach. Systematic Zoology, 35:195–203.

WILSON, D. E., AND D. M. REEDER, EDS. 1993. Mammal Species of the World: A Taxonomic and Geographic Reference. Second Edition. Smithsonian Institution Press, in Association with the American Society of Mammalogists, London and Washington, 1206 pp.

WRIGHT, S. 1978. Evolution and the Genetics of Populations. Volume 4. Variability Within and Among Natural Populations. University of Chicago Press, Chicago, 580 pp.

———. 1980. Genic and organismic selection. Evolution, 34:825–843.

ZAR, J. H. 1974. Biostatistical Analysis. Prentice-Hall, Inc., Englewood Cliffs, New Jersey, 620 pp.

ZELDITCH, M. L., R. W. DEBRY, AND D. O. STRANEY. 1989. Triangulation-measurement schemes in the multivariate analysis of size and shape. Journal of Mammalogy, 70:571–579.

ZELDITCH, M. L., F. L. BOOKSTEIN, AND B. L. LUNDRIGAN. 1993. The ontogenetic complexity of developmental constraints. Journal of Evolutionary Biology, 6:621–642.

APPENDIX I

Aethomys specimens examined. TM = Transvaal Museum, Pretoria; USNM = National Museum of Natural History, Smithsonian Institution, Washington D.C.

Aethomys chrysophilus.—Farm Al-te-ver, 1 km SSE Maasstroom, Transvaal, South Africa (22° 46′ S; 28° 28′ E): six males (TM 26474, 26541, 26557, 26559, 26612, 26684); ten females (TM 26510, 26514, 26540, 26561, 26574, 26575, 26583, 26611, 26668–69).

Aethomys granti.—Sutherland, Cape Province, South Africa (32° 23′ S; 20° 40′ E): seven males (TM 38526–28, 38530, 38532, 38536, 38538); seven females (TM 38529, 38533–34, 38537, 38541–43).

Aethomys namaquensis.—Keimoes Island, Orange River, Cape Province, South Africa (28° 43′ S; 20° 50′ E): 21 males (USNM 451913–14, 451921, 451933–34, 451941, 451948, 451950–51, 451966, 451983, 451990–91, 452000, 452002, 452019, 452028, 452039, 452041, 452045, 452055); 13 females (USNM 451915, 451924, 451956, 451992, 451994, 452003, 452006, 452016, 452020, 452031a–b, 452035, 452053).